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New Phytologist

Research

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Received: *1 March 2018*
Accepted: *2 June 2018*

New Phytologist (2018)
doi: 10.1111/nph.15304

Key words: climate feedback, drought, plant functional traits, plant secondary metabolism, thermotolerance, tree physiology, tropical forest, volatile organic compounds.

Summary

- The prediction of vegetation responses to climate requires a knowledge of how climate-sensitive plant traits mediate not only the responses of individual plants, but also shifts in the species and functional compositions of whole communities. The emission of isoprene gas – a trait shared by one-third of tree species – is known to protect leaf biochemistry under climatic stress. Here, we test the hypothesis that isoprene emission shapes tree species compositions in tropical forests by enhancing the tolerance of emitting trees to heat and drought.
- Using forest inventory data, we estimated the proportional abundance of isoprene-emitting trees (*p*IE) at 103 lowland tropical sites. We also quantified the temporal composition shifts in three tropical forests – two natural and one artificial – subjected to either anomalous warming or drought.
- Across the landscape, *p*IE increased with site mean annual temperature, but decreased with dry season length. Through time, *p*IE strongly increased under high temperatures, and moderately increased following drought.
- Our analysis shows that isoprene emission is a key plant trait determining species responses to climate. For species adapted to seasonal dry periods, isoprene emission may tradeoff with alternative strategies, such as leaf deciduousness. Community selection for isoprene-emitting species is a potential mechanism for enhanced forest resilience to climatic change.

Introduction

Variation in the metabolic traits of plant species produces a mosaic of physiological strategies at the scale of forests. To predict forest function, we must determine how metabolic traits affect both the performance of individual trees and, as a consequence, the functional composition of forests across environments (Tilman *et al.*, 1997; Moorcroft, 2006).

Isoprene emission from leaves is a secondary metabolic trait that has the potential to influence the structure and function of vegetation. Experimental studies at the level of individual plants show that isoprene protects the photosynthetic infrastructure under heat, drought and other sources of environmental stress (Peñuelas *et al.*, 2005; Behnke *et al.*, 2007; Velikova, 2008; Vickers *et al.*, 2009b; Ryan *et al.*, 2014; Tattini *et al.*, 2015). Isoprene mitigates the stress-induced accumulation of destructive oxidants (Suzuki & Mittler, 2006; Ahmad *et al.*, 2008; Vickers *et al.*, 2009a; Jardine *et al.*, 2012; Velikova *et al.*, 2016), and may also act as a rapid signaling mechanism for other defensive secondary metabolism (Fini *et al.*, 2017). A trait that mitigates cellular damage during episodic environmental extremes would improve the net lifetime carbon gain of leaves, reducing the impact to the carbon balance of the whole plant. For a tree, the carbon balance of a crown of leaves is critical when reserves are taxed towards mortality by 'carbon starvation' under high temperatures and drought (Würth *et al.*, 2005; McDowell *et al.*, 2008). The enzyme for isoprene emission is produced by approximately one-fifth of perennial plants worldwide (Loreto &

Fineschi, 2015), and by more than one-third of species in particular groups, such as tropical trees (Harley *et al.*, 2004). Despite a long history of controlled experiments (Sharkey & Monson, 2017), little is known about the costs and benefits of isoprene emission in different environments and, in particular, whether or not the capacity to emit isoprene affects species performance, and hence the ecological structure of plant communities, across space and time (Sharkey & Monson, 2014; Wang *et al.*, 2016).

The ecology of isoprene emission is likely to be a key component of ecosystem responses to climate change, especially in tropical forests, which emit more isoprene than any other biome (Guenther *et al.*, 2006) and face the likelihood of significant warming and drying this century (Kirtman *et al.*, 2013; Duffy *et al.*, 2015; Chadwick *et al.*, 2016). Observations of drought- and warming-induced mortality show that tropical tree responses vary across species and functional types (Phillips *et al.*, 2009; Enquist & Enquist, 2011; Duque *et al.*, 2015; Enquist *et al.*, 2017). Plant hydraulic traits and species variation in the temperature dependence of primary metabolism may be important drivers of these differing species responses (McDowell *et al.*, 2008; Phillips *et al.*, 2009; da Costa *et al.*, 2010; Rowland *et al.*, 2015). However, investigations of tropical forests have so far neglected how secondary biochemistry, such as isoprene emission, mediates the sensitivity of primary metabolic processes, such as leaf carbon balance, to temperature and drought.

A common approach to assess the influence of a trait on species performance is to analyze the distributions of trait values in ecological communities (Enquist *et al.*, 2015). Consistent directional shifts in community trait distributions can be strong evidence of a mechanistic relationship between the trait, plant performance and environment (Lebrija-trejos *et al.*, 2010; Violle *et al.*, 2014; Šímová *et al.*, 2015; Enquist *et al.*, 2017). Tropical forests contain an abundance and diversity of both isoprene-emitting and non-emitting tree species (Klinger *et al.*, 1998; Keller & Lerdau, 1999; Harley *et al.*, 2004). It follows that shifts in the proportional representation of emitting species—a simple community metric for isoprene—should reflect the role of isoprene in species responses to shifts in climate.

Here, we test the hypothesis that isoprene improves the performance of isoprene-emitting tree species relative to non-emitting species in tropical forests under high temperatures and drought. First, using a large biogeographic database of species and climate data, we quantify the changes in the proportional abundance of isoprene-emitting trees (*p*IE) at forest sites spanning landscape gradients of temperature and precipitation seasonality (a mean climate analog to drought) throughout the tropics. Second, we analyze temporal shifts in *p*IE attributed to differential species growth and survivorship within three distinct tropical forest sites subjected to experimental long-term warming, natural drought or experimental drought. If isoprene emission has a strong influence on species responses to climate, we can expect to see significant *p*IE shifts along climate gradients and in response to climate anomalies. More generally, our investigation tests whether the mediation of primary leaf metabolism by secondary metabolic traits, such as isoprene, is a key process structuring plant community assembly under a changing climate.

Materials and Methods

Overview

We analyzed community compositions across landscape environmental gradients using a large biogeographic database of plant inventories. We analyzed changes in tree community compositions through time at three focal sites: Biosphere 2 (USA), San Emilio (Costa Rica) and Caxiuanã (Brazil). These three sites were chosen on the basis of the availability of data and previous demonstration of community assembly responses to climate anomalies. Details for each site follow. All analyses were isolated to dicotyledonous woody tree species. Our metric of tree community composition was the estimated proportion of trees that produce isoprene (*p*IE). Species isoprene emission data were obtained by a combination of new measurements and published data. Missing data were imputed at the genus level by a probabilistic bootstrap method described later.

Datasets: study sites

We analyzed community composition changes across climate gradients over large spatial scales with a database of tree species inventories distributed across the global tropics (SALVIAS, see reference for data access; Enquist & Boyle, 2012). The SALVIAS database primarily comprises 0.1-ha tree plots for trees ≥ 2.5 cm in diameter at breast height (DBH). Climate data were obtained from the WorldClim database (Hijmans *et al.*, 2005; www.worldclim.org; resolution 30″) for SALVIAS inventory site coordinates.

We used data from The University of Arizona's Biosphere 2 tropical forest biome (B2-TF) to analyze the response of forest composition to long-term warming (for dataset, see Supporting Information Notes S1). B2-TF consists of a phylogenetically diverse assemblage of tropical trees and understory plants under a pyramidal glass enclosure (27.4 m in height by 0.2 ha at the base) (Leigh *et al.*, 1999). As a result of the high outside air temperatures and prolonged insolation of the glass enclosure during the Arizona summer, peak summertime canopy air temperatures are *c.* 10°C higher than those typical of Amazonian sites (Arain *et al.*, 2000). Precipitation and humidity are controlled in B2-TF, providing a unique decoupling of elevated temperatures from drought and leaf-to-air vapor pressure deficit. We analyzed community change from 1993 – when the installation of plants was completed (Leigh *et al.*, 1999) – to 2010 – when we conducted the latest tree inventory. By the year 2000, B2-TF was a well-developed canopy system with dynamics of ecosystem gas exchange akin to natural tropical forests (Rascher *et al.*, 2004), except potentially with an enhanced tolerance to high temperatures (Rosolem *et al.*, 2010).

We used data from the San Emilio forest dynamics plot in Guanacaste province, Costa Rica, to quantify the functional response of forest composition to natural drought (for dataset, see Enquist & Enquist, 2011). The plot is 16.32 ha in size, 240–300 m in elevation and is located at 10.84°N, 85.61°W. In total, 150 tree species have been recorded in the plot. Enquist &

Enquist (2011) showed that, between census periods (1976 and 1996), San Emilio has been witness to extended drought conditions, including the driest year yet recorded, as well as a longer term drying trend that has occurred during the life span of many of the trees within the plot. During this period, there were significant changes in tree community assembly. Functional compositions shifted towards increased proportional representation of deciduous canopy trees and species associated with more xeric environments. A thorough site description, analysis of precipitation trends and anomalies, and forest composition changes are given in Enquist & Enquist (2011).

Caxiuanã is the site of an experimental drought manipulation to natural 'terra-firme' tropical forest in the Caxiuanã National Forest Reserve in the eastern Brazilian Amazon (1°43′S, 51°27′W), administered by the Estação Científica Ferreira Penna, which belongs to the Museu Paraense Emílio Goeldi (da Costa *et al.*, 2010; Meir *et al.*, 2015). Site mean annual precipitation ranges from 2000 to 2500 mm with significantly reduced precipitation for half of the year. From January 2002 to December 2008, 50% of incident rainfall was excluded from a 1-ha treatment plot (referred to hereafter as the 'drought' plot) via translucent panels and guttering at a height of 1–2 m (Fisher *et al.*, 2007; Meir *et al.*, 2015). Several publications describe differential mortality and physiological responses between the drought plot and a 1-ha control plot across the first 7 yr of this rainfall exclusion experiment (Fisher *et al.*, 2007; da Costa *et al.*, 2010; Meir *et al.*, 2015). For example, among stems > 10 cm in DBH, tree mortality rates doubled in response to reductions in soil moisture below a threshold level of 50% relative extractable water in the treatment plot, relative to the control (da Costa *et al.*, 2010; Meir *et al.*, 2015). The dataset used in the present study is an inventory of saplings and understory woody plants to 200 cm height from a set of 20 subplots, $2 \times 2\ m^2$ each, distributed randomly throughout the drought plot, and an equivalent set in the control plot, inventoried in 2009 (Ferreira *et al.*, 2016) (for dataset, see Notes S2). Having no time series of surveys, we substitute space for time by comparing the drought and control subplots. Previous comparisons showed that the drought subplots contained significantly lower stem densities, heights and species richness, although the mechanisms of putative drought effects on these understory plants remain unexplored (Ferreira *et al.*, 2016).

Datasets: isoprene emissions inventory

We compiled a dataset of isoprene emission statuses based on measurements of 484 tropical plant species from 331 genera (for dataset, see Notes S3). Each species was labeled as an isoprene 'emitter' or 'non-emitter', based on a combination of new measurements and literature data. We included new measurements made from 26 tree species in B2-TF in 2011. Tree branches were cut and immediately re-clipped underwater to maintain xylem flow for leaf transpiration, and placed beneath LED grow lights. Transparent, 5-l 'branch enclosure bags' made of chemically inert material were used to enclose *c.* $0.5\ m^2$ of leaf area by loosely sealing the bag around the branch. Air was purified of organic compounds by charcoal filters and pumped through the bag at $1\ l\ min^{-1}$. Drawdown of CO_2 in the enclosure was measured by a LICOR Li-7000 to confirm that leaves were photosynthetically active during all measurements. Isoprene accumulation in the enclosure was determined by real-time detection with a proton transfer reaction mass spectrometer (PTR-MS). Isoprene emissions were qualitatively identified by significant increases in the mass-to-charge ratio m/z 69.

The remaining species emission data were compiled from the literature based on 'survey-type' studies reporting both emitting and non-emitting species. We identified nine such studies (Lerdau & Keller, 1997; Klinger *et al.*, 1998; Keller & Lerdau, 1999; Geron *et al.*, 2002; Greenberg *et al.*, 2003; Varshney & Singh, 2003; Harley *et al.*, 2004; Padhy & Varshney, 2005; Bracho-Nunez *et al.*, 2013). Methods for emission detection varied across studies. Data for 46 of 177 putatively isoprene-emitting species in our compiled inventory came from non-distinguishing detection methods, i.e. those unable to distinguish between isoprene and other organic compounds. In most cases, isoprene is the only compound emitted in a light-dependent manner in sufficient quantities for detection by field methods, but a small number of measurements may have detected monoterpene emissions instead (Kuhn *et al.*, 2002; Harley *et al.*, 2004). Light-dependent monoterpene emissions are likely to play similar roles to isoprene in the leaf (Vickers *et al.*, 2009a). Their limited presence in the inventory therefore might not affect the interpretation of the results. In the few cases in which two studies reported conflicting emission statuses, the species was labeled as an emitter because a false negative as a result of instrument detection limits or poor leaf health is more likely than a false positive, although species misidentifications could produce the latter. Where results from ambiguous and unambiguous detection methods disagreed, the result from the unambiguous method was assigned.

Taxonomic standardization

Taxonomic names in all taxon lists were standardized by the online application, the Taxonomic Name Resolution Service v.4.0 (TNRS, http://tnrs.iplantcollaborative.org/) (Boyle *et al.*, 2013). See Methods S1 and Notes S4 for TNRS settings, processing code and methods for automated merging of community datasets.

Assignment of emission data to species in study communities

In this study, we analyzed the variability among species in the genetically determined capacity to produce isoprene (Monson *et al.*, 2013); we did not consider the variability in the strength of emissions (data for which are much more limited). Emission values from the isoprene inventory were converted to a binary emission status (IE): 0 = species does not emit; 1 = species emits. The proportion of trees that emit isoprene (pIE) in a community was calculated by summing the product of species IE and relative abundance. Species relative abundance is calculated as the number of trees of a given species divided by the total number of trees

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in the community. Where direct species matches occurred between the inventory and a study community, IE was assigned accordingly. Where only genus-level identity was shared, an estimate of the species IE was imputed using the approach described below. Species lacking genus-level representation in the isoprene inventory did not receive imputed trait values and were excluded from all analyses.

For species lacking direct evidence of isoprene emission status, IE was imputed as follows. We used the empirical distribution of genus mean IE values (a metric of the consistency of IE within genera; Fig. S1) as the basis for a probabilistic approach to trait imputation. By iterating the probabilistic imputations and calculating community assembly results each time, we could estimate uncertainty in the results based on the uncertainty in the imputed trait values (Figs 1, 2 (insets), 3b). The imputation method and rationale follow, and are illustrated with flow diagrams in Fig. S2.

Genus mean IE ($0 \leq \bar{G} \leq 1$) reflects the probability that a random species drawn from genus G emits isoprene. However, the information value of $\bar{G}$ is limited by the number of sampled species. Although genera tend to predominantly comprise either isoprene-emitting or non-emitting species (Fig. S1), it is common to find species that deviate from their genus trend (Monson *et al.*, 2013). To impute IE for a target species (S_t), we used two sources of information: $\bar{G}$ from congeners in the IE inventory, and the distribution of $\bar{G}$ among the better sampled genera (G*) in the inventory (34 genera with known IE for at least three species). The latter was represented by three non-mutually exclusive tables of G* genus means: conserved *low* ($\bar{G}^* < 0.5$), unconserved *mid* ($0.3 < \bar{G}^* < 0.7$) and conserved *high* ($\bar{G}^* > 0.5$).

Based on its $\bar{G}$, each S_t was assigned a $\bar{G}^*$ table that would represent its IE probability. This implies limited confidence in $\bar{G}$ values in a small dataset, but reasonable confidence that $\bar{G}$ represents a particular region ($\bar{G}^*$ tables) of the distribution of $\bar{G}$ that occurs in nature. Only species S_t with $\bar{G} = 0.5$ were assigned the *mid* table. The imputed IE value for S_t was then determined by a binomial draw, with the probability of the draw equal to a genus mean ($\bar{G}_t^*$) randomly drawn from its assigned $\bar{G}^*$ table: IE (S_t) = $B(n = 1, p = \bar{G}_t^*)$.

At the end of each iteration, *p*IE was calculated for all communities, and community assembly analyses were conducted (i.e. *p*IE regressions on climate, or temporal *p*IE shifts). The collection of n_{boot} results could then be used to generate mean *p*IE estimates for each community, a distribution of uncertainty on the mean (error bars, Figs 1, 2) and uncertainty distributions around the community assembly results (regression slopes, insets Figs 1, 2; *p*IE shifts, Fig. 3b). These distributions reflect the uncertainty in the community assembly results that is attributable to uncertainty in the imputed trait values.

We believe this method to be conservative because the broad and overlapping ranges of $\bar{G}^*$ tables produce significant (but empirically grounded) variability in the assigned traits. Community differences (ΔpIE) must therefore be large to exceed the 95% confidence intervals resulting from the collection of n_{boot} ΔpIE estimates.

Community analyses: spatial

The SALVIAS plots and associated climate data were used to analyze the dependence of landscape variability in community *p*IE on mean annual temperature (MAT) and dry season length (DSL). DSL was calculated as the number of months with < 100 mm mean monthly precipitation (Holdridge, 1967; Pennington *et al.*, 2000). The SALVIAS data were filtered to include only tropical plots in which at least 25% of species had congeneric representatives in the isoprene inventory (i.e. could be assigned trait values by the method above). The data

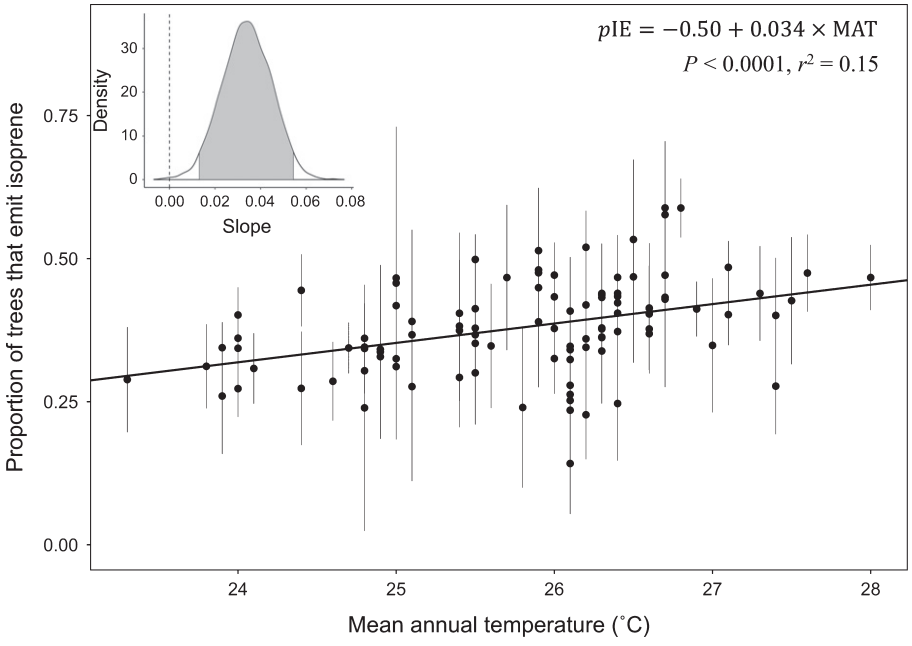

Fig. 1 The estimated proportion of trees that emit isoprene (*p*IE) at tropical forest sites increases with site mean annual temperature (MAT). Missing isoprene emission data were imputed at the genus level by a dynamic bootstrap imputation method based on the empirical pattern of genus-level trait conservatism (see the Materials and Methods section). Points and error bars are site means ± 1SD of *p*IE across all trait imputations ($T_{i:n}$). The linear regression line represents mean *p*IE values ($p\text{IE} = -0.50 + 0.034 \times \text{MAT}$, $P < 0.0001$, $r^2 = 0.15$). The inset figure shows the distribution of linear regression slopes from each T_i. The edges of the shaded region are the 95% confidence intervals. Among $T_{i:n}$, 99.8% of slopes were positive.

were further filtered to include low-elevation sites only (≤ 300 m altitude) to avoid confounding effects of elevation and temperature. Filtering resulted in 103 informative plots (for a table of sites used and associated meta data, see Notes S5). As a result of the high diversity of tropical forests, a large majority of species required imputation of isoprene emission status. There were an estimated 4591 species in the final set of SALVIAS plots used. Of these species, 158 (3.4%) were assigned a species-level IE status, and 1785 (39%) received imputed values. IE status could not be assigned to the remaining 2648 species (58%), which were excluded from the analyses. Because the sets of species included vs excluded from the analyses are determined by their genus-level overlap with our compilation of survey-type forest inventories of species IE statuses, each set is expected roughly to be a random selection of tropical diversity. However, haphazard species sampling in forest inventories is affected by relative abundances of different clades, and therefore our analyses probably under-represent rare genera.

The average expected relationship between *p*IE and MAT or DSL was calculated with a simple linear regression based on the plot mean *p*IE values across trait imputations (solid regression lines, Figs 1, 2). Regression significance relative to trait uncertainty was determined from the distribution of regression slope values from all imputation iterations (insets, Figs 1, 2). A multiple regression was conducted to account for a slight interactive effect ($pIE = b_0 + b_1 \times MAT + b_2 \times MAT \times DSL$; dashed regression lines for high and low temperatures, Fig. 2). Site mean *p*IE values were approximately normally distributed in the middle of the range and not truncated at 0 or 1, justifying a standard linear regression approach on proportion data (Fig. S3).

Community analyses: temporal

We assessed changes in community composition through time at three focal sites subjected to warming (Biosphere 2), natural drought (San Emilio) and experimental drought (Caxiuanã) (Fig. 3b). Composition shifts were analyzed in two ways to reflect two independent sources of uncertainty: the null expectation for non-selective community assembly, and the uncertainty associated with the imputation of missing trait values. For null community analyses, species traits were fixed by their respective IE means across trait imputations ($0 \le IE \le 1$). Non-binary, species-mean IE values propagate to a probabilistic estimate of *p*IE. Separately, the contribution of trait imputation to uncertainty in *p*IE shifts (Δ*p*IE) was assessed by comparing the distribution of Δ*p*IE across imputation iterations to 0, i.e. no shift (light gray density distributions, Fig. 3b).

For Biosphere 2 and San Emilio, *p*IE at the end time point (T_2) was compared with a null distribution of *p*IE for that time point. The null distribution was based on bootstrap simulations of random species composition changes between the first time point (T_1) and T_2. In Biosphere 2, given that only one species (*Pachira aquatica*, isoprene emitter) recruited self-sustaining

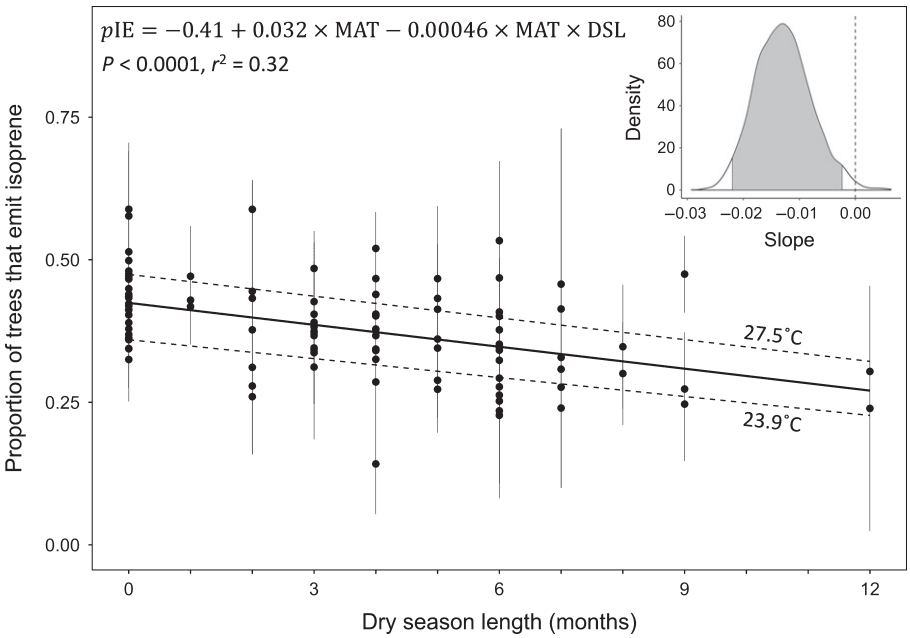

Fig. 2 The estimated proportion of trees that emit isoprene (*p*IE) at tropical forest sites decreases with site dry season length (DSL; number of months per year with precipitation < 100 mm). Missing isoprene emission data were imputed at the genus level by a dynamic bootstrap imputation method based on the empirical pattern of genus-level trait conservatism (see the Materials and Methods section). Points and error bars are site means ± 1SD of *p*IE across all trait imputations ($T_{i:n}$). The solid linear regression line shows the relationship between mean *p*IE values and DSL ($pIE = 0.43 - 0.013 \times DSL$; $P < 0.0001$, $r^2 = 0.2$). The dashed regression lines show the modeled relationship from a multiple linear regression accounting for a slight interactive effect of mean annual temperature (MAT) and DSL ($pIE = -0.41 + 0.032 \times MAT - 0.00046 \times MAT \times DSL$, $P < 0.0001$, $r^2 = 0.32$). The two modeled temperatures are the 2.5% (23.9°C) and 97.5% (27.5°C) quantiles of the MAT distribution across all sites. The inset figure shows the distribution of linear regression slopes of *p*IE on DSL alone from each T_i. The edges of the shade region are the 95% confidence intervals. Among $T_{i:n}$, 99.2% of regression slopes were negative.

seedlings over the census interval used in this study, recruits were not included in the analyses. Therefore, random community change was simulated by random mortality only. Null communities for T_2 were generated by randomly selecting a number of individual trees from the T_1 community equal to the number of trees present at T_2, sampled without replacement. 1000 iterations were sufficient to saturate the range of possible outcomes. The significance of non-random shifts in *p*IE (Δ*p*IE) was determined by subtracting each pIE_{null} from pIE_{obs} at T_2, and comparing the resulting distribution of Δ*p*IE to 0 (dark gray density distributions in Fig. 3b). Of Biosphere 2 species, 41 (54%) were assigned a species-level IE status, including all 2010 trees, and 16 (21%) received imputed values. IE status could not be assigned to 19 species (25%).

The San Emilio site is a natural forest open to recruitment of individuals into the measured size classes (DBH ≥ 10 cm) from smaller sizes and from the regional species pool (for trees that could quickly establish and grow to 10 cm DBH within the 20-yr census interval). Similar to Biosphere 2, T_2 null communities were generated by randomly sampling a number of trees from the T_1 community equal to the number observed at T_2. In this case, trees were sampled with replacement, which allowed a representation of recruitment potential. 10 000 iterations were applied. This model assumes that the T_1 community represented the

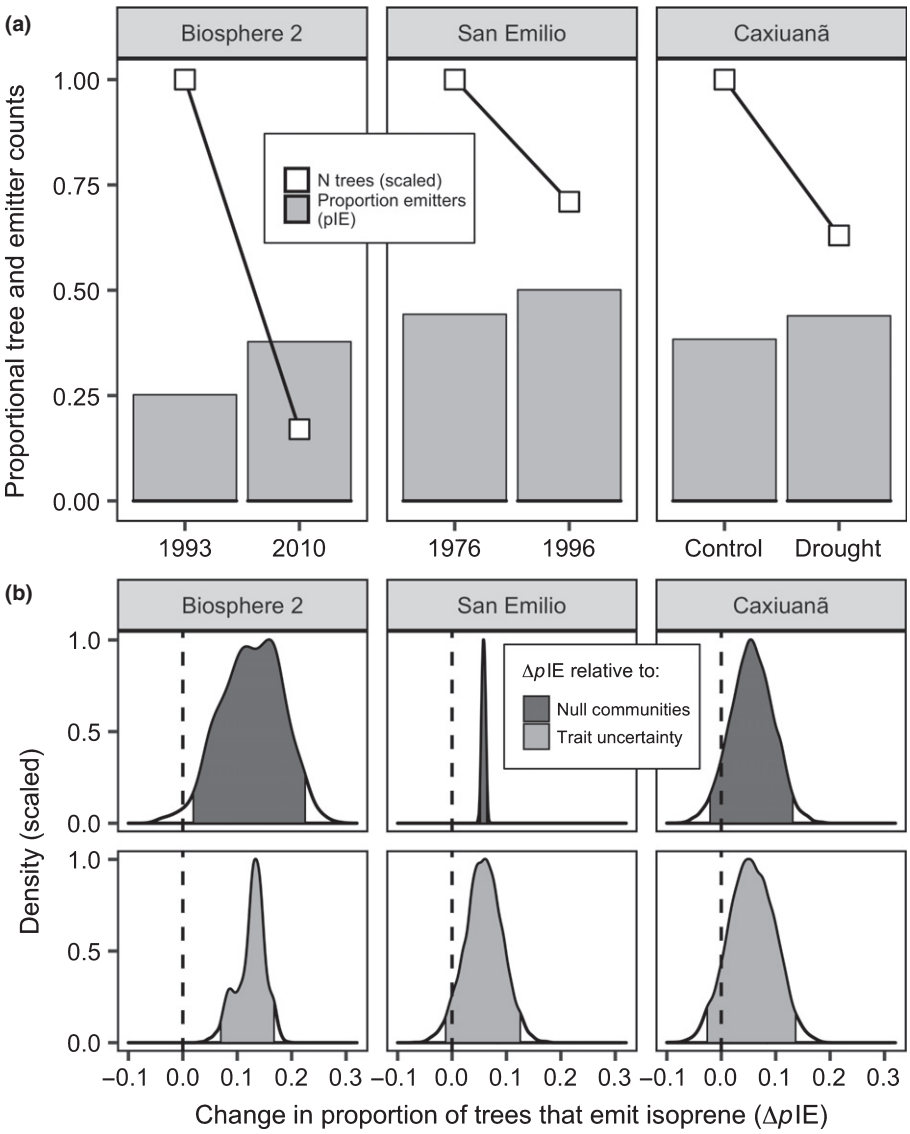

Fig. 3 Analyses of tree community change at three tropical forest sites responding to warming (Biosphere 2), natural drought (San Emilio) and experimental drought (Caxiuanã). (a) Relative changes in stem density and the proportion of trees that emit isoprene (*p*IE). (b) Density diagrams representing the distribution of estimated change in *p*IE (Δ*p*IE) according to two models. Positive values represent increases in *p*IE from time 1 (or control plot) to time 2 (or drought plot). White regions are the 2.5% tails. For Biosphere 2 and San Emilio, the dark gray distributions comprise Δ*p*IE relative to null communities representing non-selective changes in species composition. For Caxiuanã, where treatment groups (drought and control) are substituted for time, the dark gray distributions comprise Δ*p*IE from a resampling analysis of drought and control communities. The light gray distributions comprise Δ*p*IE calculated from each iteration of probabilistic imputations of isoprene emission status to unmeasured species.

range of trait values available among potentially recruiting trees. This is a reasonable assumption given that most recruits to T_2 will have come from smaller size classes, which are likely to mostly comprise progeny of T_1 adults. Of San Emilio species, 23 (15%) were assigned species-level IE status, and 65 (41%) received imputed values. IE status could not be assigned to 69 species (44%).

For Caxiuanã, community change was assessed by comparing *p*IE between control and drought treatment groups. Subplots ($n = 20$ each) were used as replicates for comparing treatment *p*IE by *t*-test. For visual representation, a distribution of Δ*p*IE was generated by resampling 50% of trees from each treatment with replacement 10 000 times (Fig. 3b). Of Caxiuanã species, eight (5%) were assigned a species-level IE status, and 82 (55%) received imputed values. IE status could not be assigned to 58 species (39%).

Results

The distribution of isoprene-emitting tree species across low-elevation tropical forests was structured by climate. Site mean *p*IE significantly increased with MAT at a rate of 0.034 per °C ($pIE = -0.50 + 0.034 \times MAT$, $P < 0.0001$, $r^2 = 0.15$, Fig. 1), a 54% increase from the lowest to highest site MAT. The sign of the regression slope was robust to the uncertainty in imputed isoprene emission statuses to unmeasured species. Linear regressions from each iteration of probabilistic trait imputations produced a distribution of slope values that significantly excluded zero (99.8% positive; inset, Fig. 1). Contrary to the hypothesized benefit of isoprene to trees under all forms of drought, site mean *p*IE significantly decreased with DSL at a rate of −0.013 per dry month ($pIE = 0.43 - 0.013 \times DSL$, linear regression, $P < 0.0001$, $r^2 = 0.2$, Fig. 2), a 36% decrease from the lowest to highest site DSL. Slope values across trait imputations significantly excluded zero, with 99.2% negative slopes (inset, Fig. 2). A multiple regression accounting for a slight interaction between MAT and DSL was a stronger predictor of site mean *p*IE ($pIE = -0.41 + 0.032 \times MAT - 0.00046 \times MAT \times DSL$, $P < 0.0001$, $r^2 = 0.32$; dashed lines, Fig. 2). A lack of correlation between site MAT and DSL explains the near independence of *p*IE responses (Fig. S4). To provide a result more applicable to forest isoprene emission models, a separate multiple regression was conducted with *p*IE scaled by species relative basal area (a proxy for relative leaf area) instead of numerical abundance ($pIE_{basal} = -0.62 + 0.041 \times MAT - 0.00046 \times MAT \times DSL$, $P < 0.0001$, $r^2 = 0.27$; Figs S5, S6). Regression coefficients from all models are summarized in Table S1.

Temporal analyses of all three focal communities showed a decrease in stem densities and an increase in *p*IE in response both to warming (in agreement with the spatial analyses) and drought (in contrast with the spatial analyses) (Fig. 3a). The increase in *p*IE was not always significant according to the models of non-selective community change and trait imputation uncertainty (Fig. 3b). Smaller *p*IE shifts in the drought sites were also obscured by broader trait uncertainty, compared with the high-temperature site (Fig. 3b). The proportions of analyzed species requiring imputed emission statuses were 74% and 91% for San Emilio and Caxiuanã, respectively, compared with 23% at Biosphere 2.

In the artificially warmed site, Biosphere 2, the number of trees decreased by 83%, from 300 trees in 1993 (76 species) to 51 trees in 2010 (25 species). The estimated *p*IE increased by 52% from 0.25 to 0.38. It should be noted that the majority of trees in 1993 were saplings, and significant mortality was expected as growing trees competed for space. The remaining trees in 2010 and thereafter formed a healthy and structurally diverse canopy. The increase in *p*IE was significant according to both uncertainty models. Under the null community model of non-selective tree mortality, pIE_{obs} in 2010 was greater than 98.5% of pIE_{null}. Across iterations of trait imputation, 100% of Δ*p*IE ($pIE_{2010} - pIE_{1993}$) were positive.

In the natural drought site, San Emilio, the tree stem count decreased by 29%, from 23 677 trees in 1976 (148 species) to 16 787 trees in 1996 (138 species). Estimated *p*IE increased by 14% from 0.44 to 0.50. The observed *p*IE shift was significantly greater than that expected from null communities representing non-selective mortality and recruitment, with pIE_{obs} in 1996 greater than 100% of pIE_{null}. However, the *p*IE shift was not significant relative to uncertainty in imputed trait values. Across iterations of trait imputation, 94.8% of Δ*p*IE ($pIE_{1996} - pIE_{1976}$) were positive.

In the experimental drought site, Caxiuanã, the tree stem count was 47% lower in the drought plot (348 trees, 83 species) compared with the control plot (654 trees, 125 species). Estimated *p*IE was 16% higher in the drought plot (0.44) compared with the control plot (0.38). The positive shift was not significant according to either uncertainty model. A *t*-test comparing *p*IE between drought and control subplots showed a non-significant difference ($P = 0.13$), comparable with the resampling analysis shown in Fig. 3(b) (92.2% positive Δ*p*IE). Across iterations of trait imputation, 90.6% of Δ*p*IE ($pIE_{drought} - pIE_{control}$) were positive.

Discussion

Our results support the hypothesis that isoprene emission influences tree community assembly by affecting the response of species performance to the environment. We found evidence for significant biogeographical structuring of the proportion of trees that emit isoprene (*p*IE) in relation to MAT and DSL (Figs 1, 2). The amount of variation in *p*IE explained by each environmental variable alone is in the range of other known climate–trait relationships, whereas the combined model r^2 (0.32) is relatively high (Moles *et al.*, 2014). Differential performance of isoprene-emitting and non-emitting functional groups is supported by community shifts observed in at least two (warmed and natural drought; Biosphere 2 and San Emilio, respectively) of the three focal sites (Fig. 3). The intriguing contrast in the response of *p*IE to drought (increasing) and DSL (decreasing) suggests that the adaptive value of isoprene depends on the duration of water deficit, or the compatibility of isoprene with other plant traits. The mechanisms of community assembly that distinguish the two types of analyses conducted – spatial and temporal – are differentiated by time scale. Biogeographical assembly is a slow

process, involving gradual dispersal and evolution (Pennington *et al.*, 2009; Bush *et al.*, 2011). By contrast, climate anomalies drive rapid shifts characterized by differential mortality and a reduction in tree density and species richness (Enquist & Enquist, 2011; Feeley *et al.*, 2013).

Our results provide a unique line of evidence in support of the hypothesis that isoprene enhances the thermal tolerance of photosynthesis in plants that produce it. Although the thermal tolerance hypothesis is widely supported, studies finding weak or conflicting evidence have generated controversy (Sharkey & Yeh, 2001). That is a result in part of methodological issues. The traditional experimental approach is to attempt to isolate the effect of isoprene by generating control and treatment groups within plant species. For example, isoprene emission can be regulated by genetic manipulation (Behnke *et al.*, 2007; Ryan *et al.*, 2014), or by introducing metabolic pathway-specific poisons to inhibit its synthesis (Zeidler *et al.*, 1998; Sharkey *et al.*, 2001). However, the isoprene effect is never truly isolated, as manipulating the pathway for isoprene synthesis affects a diversity of other cellular processes (Possell *et al.*, 2010; Velikova *et al.*, 2014). By contrast, in our macroecological approach, the effect of isoprene emission on tree performance emerges from the collective outcome of diverse species assemblages that vary across sites (Brown & Maurer, 1989). The positive relationship between *p*IE and temperature is consistent with a benefit of isoprene that is generalizable across species in their natural ecological context.

Community shifts at the two drought sites showed a weaker favoring of emitters (*p*IE increased by 14–16%) with less statistical confidence than at the high-temperature site (*p*IE increased by 52%). It is possible that reducing trait uncertainty with more species measurements would improve confidence in the positive *p*IE shifts with drought (Fig. 3b). The question of whether and how isoprene helps plants under drought has received less experimental attention than thermal tolerance. There is evidence that isoprene reduces oxidative damage to the photosynthetic machinery during drought, resulting in improved photosynthetic recovery rates on re-wetting (Ryan *et al.*, 2014; Tattini *et al.*, 2015; Velikova *et al.*, 2016). Oxidant accumulation can occur as a result of higher temperatures (Suzuki & Mittler, 2006), which tend to accompany drought (Toomey *et al.*, 2011), or as a result of unused light energy (Niyogi, 2000). The tradeoff is that isoprene can exert an increasing carbon drain on growth as drought progresses because emission rates typically decline more slowly than photosynthetic rates (Fang *et al.*, 1996; Brüggemann & Schnitzler, 2002; Seco *et al.*, 2015; Fini *et al.*, 2017). The combination of sunnier days and reduced transpiration causes elevated leaf temperatures, which also drive higher emission rates (Potosnak *et al.*, 2014; Tattini *et al.*, 2015). The allocation of photosynthetically fixed carbon to isoprene during drought can exceed 10% (Tattini *et al.*, 2015), and 50% in extreme cases (Sharkey & Loreto, 1993; Fang *et al.*, 1996). Alternative drought strategies with lower energetic costs may often be more competitive. For example, at San Emilio, and in a similar study in Africa, forest composition shifts favored trees with deciduous leaf habits (Enquist & Enquist, 2011; Fauset *et al.*, 2012). The role of isoprene in drought tolerance probably depends on other leaf traits, and may be constrained by the leaf carbon economic strategies of each species.

A competitive advantage of drought strategies that are less carbon intensive could also explain the decrease in *p*IE towards seasonally drier sites. A previous study in the African tropics found an analogous decrease in *p*IE (as a percentage of species) from forest to adjacent savanna (Klinger *et al.*, 1998). In contrast with drought, the regularity of seasonally dry periods allows for phenological adaptation (Eamus, 1999). Deciduous tree species are adapted to avoid dry season high temperatures and water deficit by dropping leaves. Stress avoidance leaves little role for the benefits of isoprene. The proportion of trees with a deciduous leaf habit in tropical forest linearly increases with the length of the dry season (Reich, 1995). The observed decrease in *p*IE with DSL is therefore consistent with a decreasing proportion of evergreen trees that require strategies to tolerate the dry season. Whether isoprene is an increasingly dominant strategy among evergreen trees towards drier sites is a compelling question for which we have insufficient data coverage to resolve.

The sites in our temporal analyses represent climatic anomalies, with changes in community structure driven primarily by differential mortality. In other words, the functional strategies best suited to the new environment increase in relative abundance simply by persisting whilst others disappear. Our biogeographical analyses represent the much slower assembly processes of long-distance dispersal and evolution. Our results suggest that a warming climate will favor isoprene-emitting species over both long and short timescales (Figs 1, 3). A drying climate may initially increase the relative abundance of emitters (Fig. 3), but, if drought is seasonally regular, the emitters will be gradually displaced by species with more competitive strategies (Fig. 2). However, in an era of rapid climatic change and increasing barriers to dispersal, near-term community shifts may be more relevant to the forecasting of the feedbacks between human activities, ecosystem functions and biological diversity.

To understand the precise mechanisms of selection for and against isoprene-emitting species in particular environments, we require a more detailed understanding of how isoprene fits into the larger context of whole-plant strategies of temperature and drought tolerance. For example, traits such as leaf size, density and light absorptivity all affect the leaf temperatures experienced by different species (Michaletz *et al.*, 2016; Wright *et al.*, 2017). Leaves that are more resistant to drought-induced embolism tend towards higher density (Zhu *et al.*, 2018) and, consequently, thermal mass, but can maintain the cooling effects of transpiration for longer in a drought (Méndez-alonzo *et al.*, 2016; Lin *et al.*, 2017). Is isoprene used by trees predisposed to operate under higher temperatures and hydraulic strain, or is it a buffer against transient stress for more conservative strategies? For drought tolerance, the answer may depend on whether isoprene is more important for the mitigation of biochemical perturbations caused by sustained photosynthesis at elevated temperatures (Suzuki & Mittler, 2006), or suspended photosynthesis at elevated light (Niyogi, 2000; Fini *et al.*, 2017). The role of isoprene in climate adaptations may also depend on the potential emission rates specific to each species (Monson *et al.*, 1995). Species with

low emission rates might be less favored under high temperatures, but suffer less carbon expense during drought. The majority of available data for tropical species are from semi-quantitative measurements made under ambient conditions (e.g. Klinger *et al.*, 1998; Harley *et al.*, 2004). More standardized measurements are needed to explore the costs and benefits of different emission rates to species climatic tolerances.

One challenge to exploring integrated trait and environment relationships to isoprene emission stems from the lack of data available for the majority of species. Scaling species traits up to regional patterns and processes, therefore, will always require some imputation (as in, for example, ter Steege *et al.*, 2006; Baker *et al.*, 2009), as no trait can be sampled for all of the > 40 000 tropical tree species (Slik *et al.*, 2015). Traditional imputation approaches use taxonomic averaging, including for isoprene (Benjamin *et al.*, 1996; Karlik & Winer, 2001). Techniques that provide estimates of uncertainty of imputation, such as the new bootstrap method developed here, provide a means of assigning confidence to predictions of forest compositional change. Nevertheless, the data that inform our imputation method are limited. Our compendium of tropical isoprene inventories comprises nearly 500 measured species, *c.* 1% of tropical tree diversity (Slik *et al.*, 2015). There is a clear need for more species measurements, especially at sites along environmental gradients that can be used to independently test the conclusions from this study. It may also be possible to narrow imputation uncertainty by incorporating other layers of information, such as how the isoprene trait is structured across plant trait strategies and the phylogenetic tree (Taugourdeau *et al.*, 2014; Schrodt *et al.*, 2015; Swenson *et al.*, 2017). New measurements should target informative species groups: those that maximize overlap with other trait datasets, improve landscape representation (e.g. Amazon hyperdominant species; ter Steege *et al.*, 2013) and inform evolutionary hypotheses to resolve the distribution of isoprene in the plant phylogeny (Monson *et al.*, 2013; Dani *et al.*, 2014).

The results from this study can be directly incorporated into forest isoprene emission models to improve estimates of the impact of *p*IE shifts on present and future climate (Guenther *et al.*, 2006; Sharkey & Monson, 2014; Wang *et al.*, 2016, 2017). In the atmosphere, isoprene emissions from forests affect chemistry and aerosol formation, influencing cloud dynamics and albedo (Carslaw *et al.*, 2010), especially over strongly emitting biomes, such as tropical forests (Guenther *et al.*, 2006). The conventional approach for the estimation of forest emission potentials in models simply multiplies *p*IE by an estimate of relative leaf area to produce a single 'emitter fraction' for each biome (Geron *et al.*, 1994; Guenther, 1997). *p*IE is obtained from coarse regional estimates (Loreto & Fineschi, 2015) or from small-scale surveys conducted for site-specific modeling (Harley *et al.*, 2004), and leaves are assigned an average emission capacity to scale modeled emission rates (Guenther *et al.*, 2006). Our results can improve on this approach by providing a quantifiable expectation for landscape variation in emitter fraction that is dependent on environment (Figs 1, 2) and, if known, on species composition. On average, climate anomalies increased *p*IE at our three temporal sites by 27% (Fig. 3). If directly translated to emitter fraction (and assuming constant total leaf area and leaf emission capacity), this implies a 27% increase in forest emission potential. In the Supporting Information of this article, we include a version of our biogeographical model that is scaled by species relative basal area as a direct representation of emitter fraction for ecosystem models (Figs S5, S6; Table S1).

An understanding of which traits confer tolerance of future climate conditions can help us anticipate changes in biodiversity and ecosystem functions. This study highlights the role of a critical leaf secondary metabolic trait in landscape-scale ecosystem processes. Our work extends previous research into the effect of isoprene emission on the functioning of individual leaves, to investigate its ecology and how it structures tropical tree community assembly across environments. Our results provide evidence that isoprene can help emitting tree species to tolerate a hotter climate, and may help some species during drought. The mapping of isoprene to community assembly provides a quantitative foundation for the modeling of forest emission potentials across landscapes and through time. As traits such as isoprene shape plant species responses to climate, shifting species compositions will shape ecosystem functions on a warming planet.

Acknowledgements

We thank K. Jardine for guidance in isoprene emission measurements at Biosphere 2, and R. K. Monson and three anonymous reviewers for constructive comments on the manuscript. Financial support for this study was provided to: T.C.T. and S.R.S. by grants NSF-PIRE #OISE-0730305, USDOE #3002937712, NASA #NNX17AF65G and the University of AZ Agnes Nelms Haury Program in Environment and Social Justice; to M.N.S. and S.R.S. by NASA-ESSF #NNX14AK95H; to C.V. by ERC-StG-2014-639706-CONSTRAINTS; to I.S. by Grant Agency of the Czech Republic #16-26369S; and to P.M. by NERC # NE/N006852/1 and ARC #DP170104091.

Author contributions

T.C.T, M.N.S., B.B., J.v.H. and S.R.S. designed the research; T.C.T. conducted field and laboratory work in Biosphere 2; B.B., I.S., P.B.d.C., L.V.F., A.C.L.d.C., P.M. and B.J.E. provided data; T.C.T., S.M.M. and B.B. analyzed the data; T.C.T, S.M.M., M.N.S., B.B., C.V., J.v.H., I.S., B.J.E. and S.R.S. wrote the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article:

Fig. S1 Genus-level conservatism of isoprene trait represented by histogram of genus-averaged binary emission statuses.

Fig. S2 Flow chart describing the method for probabilistic imputation of isoprene emission values to unmeasured species, and evaluation of community assembly results relative to trait uncertainty.

Fig. S3 Distribution of site mean *p*IE values across trait imputations justifies simple regression on proportion data.

Fig. S4 Scatter plot showing no relationship between site mean annual temperature and dry season length.

Fig. S5 A basal area-scaled version of Fig. 1 (*p*IE by mean annual temperature) as representation of 'emitter fraction' for forest emissions models.

Fig. S6 A basal area-scaled version of Fig. 2 (*p*IE by dry season length) as representation of 'emitter fraction' for forest emissions models.

Table S1 Coefficients from all simple and multiple regressions relating site *p*IE to climate for use in forest emissions modeling

Methods S1 Methods for taxonomic name standardization and community dataset integration.

Notes S1 Biosphere 2 tropical forest inventory data.

Notes S2 Caxiuanã plant inventory data.

Notes S3 Tropical isoprene emitter inventory.

Notes S4 Taxonomic name resolution R script.

Notes S5 SALVIAS plots meta data.

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